THE ORGANIZATION OF THE ECOLOGICAL INVESTIGATION OF THE PHYSIOLOGICAL LIFE-HISTORIES OF PLANTS [1]

Upon several occasions I have expressed the belief that the first need of plant ecology is the determination of the physiological life-histories of the forms concerned. I propose now to explain more fully what I mean.

First, it is essential to note our changing conception of ecology. It is not long since we sought a use for every detail of plant structure and habit, and, correlatively, assumed that these had been developed in some kind of causal touch with the environmental conditions they were supposed exactly to fit. This was causal, or historical, adaptation, and it was the logical product of the Darwinian assumption of a struggle for existence so keen as to make even minutiae determinative of the survival or extinction of whole organisms, and through them of entire species. Now, partly because of the work of DE VRIES, but partly, I venture to assert, because of the studies of ecologists themselves, we are ceasing to require utility in details of structure and habit, and are coming to believe that such details may be determined by factors wholly independent of the immediate environment. This newer view does not exclude the possibility of causal or historical adaptation in details, but it accepts the probability of a very different origin and meaning of those details. And this different non-causal origin and meaning of the relation between the details of structure-habit and environment may be either of these two. First, the adaptation may be real but a matter of accident or coincidence, the details arising from internal or other irrelative causes and finding their appropriate environment by a process of sifting. Second, the details, however arisen, may have no positive relationships whatever with the environment, but, not happening to run counter to any very potent feature of that environment, they exist by toleration. In brief, while adaptation as a broad, a general, a generic matter is a reality and rests upon a certain historical or causative basis, adaptation as an exact, a minute, a specific matter is quite different; it may be causative, but it is more often coincidental or tolerative. The ecology of the future will be, primarily, not a search for utilities, but an analysis of meanings.

I emphasize this matter thus fully because I believe that in the phase of ecology of greatest present-day interest, viz., physiognomic ecology, the study of the factors determining the features of vegetation, it will prove most illuminating. A great deal of our supposed adaptation of vegetation

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to habitat is, I have no doubt, not adaptation in the old sense at all, but is a sifting-in of forms whose characters have been elsewhere and otherwise determined, but which happen to match, either by coincidence or by toleration, with the physical conditions prevailing in that habitat. So far do I consider this true that I think our best working hypothesis in this field is this: any plant stands where it does for the reason that the physical demands made by the structure and habit it happens to possess overlap in some degree the physical conditions prevailing in that place, and the better they match the more nearly does the plant find its optimum, and the worse they match the more slender is the hold of the plant upon that place. Now the study and measurement of the physical factors of environments is steadily progressing; it behooves us to study and measure the physical demands of the plants in order that we may be able to compare the one with the other. This is the crux of what I mean by the need for physiological life-histories of plants.

I come now to the practical part of the subject. I assume that the plant is a bundle of physical needs, and that our aim is to determine what and how great these are. Then these things are needful:

1. We must devise methods and instruments, for the most part autographic, for measuring and recording each physiological process. This, indeed, we are doing, but must do more and better.

2. We must develop a system of standard units for each physiological process, such as will permit their exact expression and their comparison. We already measure photosynthesis in grams per square meter of surface per hour, and are approximating to similar definite units for respiration and transpiration. We must develop similar systems for the other processes. Further, we must develop methods of graphic expression of such data in order that they may be readily matched against the graphic results supplied by study of the environments. In most cases these will doubtless work themselves out in the form of minimum-optimum-maximum curves, but it will not be enough to make these curves represent means or averages; they must express the range of frequency from the mean, which can be done by means of shaded or penumbrate graphs, in which the mean forms the dark center and the shading merges off thence to the extremes.

3. We must not confine our measurements to those invisible processes in the protoplasm which we commonly associate with physiology, but must include structure which is simply an external and visible manifestation of physiological operations, a tool which physiology forges as an aid in its processes. Does a plant produce a long tap-root? That is because, for reason sufficient unto itself even though unknown to us, the protoplasm

of that plant extends itself deep into the ground; the structure is a visible physiological result, and is to be measured and expressed like the other physiological processes.

4. We must especially learn to distinguish and to express to what degree the various physiological processes are plastic to the action of stimuli, and to what extent are limited by heredity.

5. We must classify the physiological processes for study. Ecologically speaking there are four critical periods in the life-cycle of a plant. These are (*a*) the germination of seed or spore, (*b*) the orientation of the seedling whereby the plant gains a grip upon its immediate surroundings, (*c*) the expansion of the adult, and (*d*) flowering and fruiting, or sporification. It is not enough that the plant can match an environment in three of these; it must match in all four. I have no doubt dissemination brings regularly into a certain habitat some plants which can germinate their seeds there, flourish as adults, flower and fruit, but in which the seedling stem and leaves cannot stand the light and heat to which they are exposed, or in which the seedling root cannot reach the permanent water supply, and accordingly that kind of plant cannot exist in that habitat. I think it is some such determinant which brings it to pass that, of all the trees whose seeds are brought upon the Miscou sandplains from the neighboring upland, not one can exist there except the white spruce. I think many peculiarities of ecological distribution are determined by just such single seemingly insignificant causes. But to explain such cases we must know the plants, and must know them throughout their life-cycles; and this is the essence of a knowledge of physiological life-histories.

The particulars of a classification of physiological-ecological processes can be worked out only by experience; but following are some of the more important topics:

A. Germination of the seed:

Amount of water requisite, least and best, and duration thereof.

Temperature requisite, minimum, optimum, and maximum, and rate under each.

Light, whether necessary, injurious, or indifferent.

Quality of water requisite; how much of salts it may contain.

Free oxygen requisite, or can it germinate under water?

Germinates on the surface or needs planting, and why?

B. The seedling life:

Root system; ordinary form and size and limits of irritable adjustment.

Stem and leaf system, ordinary form and size, and limits of irritable adjustment.

Temperature conditions.

Water, amount and quality requisite.
Light, amount requisite for photosynthetic work, least, best, and most.
How far carried by stored food, and when its own nutrition begins.

C. Adult life:
Demand for water, and interadjustment of absorption, transfer, and transpiration.
Demand for the important minerals.
Dependence upon mycorhiza or other organic aids.
Form and size of vegetative parts, and plasticity thereof.
Temperature demands.
Light demands.

D. Flowering and fruiting (sporification):
Conditions determining beginning of reproduction.
Vegetative powers of reproduction.
Arrangements for uniting the sexes, and extent of dependence thereon.
Duration of vitality, and the resting period of the seed.
Dissemination conditions.

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